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Reactions of the fauna on the bark of trees to the frequency of fires in a North American savanna

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Summary. The arthropod communities living on the bark of the oak species *Quercus macrocarpa* and *Q. ellipsoidalis* were investigated in a North American oak savanna. Differences were found in the community structure of the arthropods living on the bark of these two tree species, although they have the same fissured bark type. In the North American oak savanna ecosystem the most important disturbance factor is fire, which maintains species richness. Highest numbers of species and specimens were found at moderately disturbed sites. Three main ecological groups of arthropods living on the bark of trees can be distinguished in relation to the degree of disturbance: (1) Inhabitants of bark of trees restricted to undisturbed sites: they do not occur in fire-disturbed areas; (2) Inhabitants of bark of trees adapted to a moderate degree of disturbance: many species occur in high numbers only in moderately disturbed areas; and (3) Specialist inhabitants of bark of trees in heavily disturbed areas. The number of specimens of these species increases per trunk with the frequency of disturbance.

Key words: Fire – Oak savanna – Tree bark – Arthropod fauna – North America

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Tree trunks are important structural elements in forest and savanna ecosystems. Tree bark has two main ecological functions. Thermal properties of bark enable trees to survive disturbances in the ecosystem (Nicolai 1986, 1987a, 1989a, b); e.g., high insulation properties help trees to survive fires (Nicolai 1990). After disturbances in forests (e.g., after fire or wind throw) tree species with different bark types settle the areas. This is part of the cyclic mosaic concept of ecosystems (Lieberman and Lieberman 1987; Nicolai 1986, 1989a, 1990; Pickett 1976; Pickett et al. 1989; Pickett 1989; Swaine and Hall 1988; Remmert 1987, 1991; Torquebian 1986.) The second ecological function of bark is its significance as a habitat for arthropods. In a central European forest ecosystem about 100 arthropod species were found to live exclusively on bark and different bark types provided different habitats (Nicolai 1986, 1987a). Similar results were found in two different African ecosystems (Nicolai 1989a). In this study I analyzed the effects of the disturbance factor, fire, on the arthropod communities living on the bark of trees in a North American oak savanna. Arthropod populations in heavily burned and moderately burned conditions (reflecting frequency of fires) were compared with an adjacent control area (unburned) with similar soils and climate.

Materials and methods

Study site

The investigations were carried out during summer 1989 in a North American oak savanna in the Cedar Creek Natural History Area, Minnesota, U.S.A. (45° 25′ N, 93° 10′ W). In this area a fire program has existed since 1964, which is described in detail by Irving (1985) and Tester (1989). Experimentally manipulated burns are implemented on nine sites (2.6–27.5 ha), and on the different sites burns are carried out at different frequencies (Tester 1989). Other studies describe the history of the area (Hudson 1985; Pierce 1954), soils (Grigal et al. 1974; Grigal 1985), vegetation (Moore 1973), and the effects of fires on the oak savanna ecosystem (White 1983); there are also some studies on insects (Haarstad 1985). The tree species of the oak savanna in the Cedar Creek Natural History Area are mainly *Quercus macrocarpa* and *Q. ellipsoidalis* (White 1983).

Fauna

Three sites with different frequencies of fire were selected: an area which was burned nearly every year during spring (20 times since 1964, last burn prior to study: 1988); an area with a moderate frequency of burns during spring (3 times since 1964, last burn prior to study: 1983); and a control area which has not been burned since 1964. In these sites the bark fauna of *Q. macrocarpa* and *Q. ellipsoidalis* was investigated. Both oak species have a fissured bark type. The animals were collected by hand. From 20 cm up to 2.5 m above the ground all animals on the trunk around the whole tree were collected in pooters. The animals were preserved in 70% ethanol. Tree species, time of day, weather conditions, girth and position of the tree, and behaviour of the bark fauna was noted. The animals were sorted and counted. Statistics follow Mühlenberg (1989).

Results

Table 1 presents a summary of the dominant arthropod groups (>5% of all collected arthropods, $n = 14\,960$) living exclusively on the bark of *Q. ellipsoidalis* and *Q. macrocarpa* in the Cedar Creek Natural History Area. Both oak species have a fissured bark tpye. In the area burned 20 times since 1964, Chironomidae (Diptera) made up 51.5% and Lepidoptera 21.9% of all arthropods collected on the bark of *Q. macrocarpa*. In the area burned 3 times since 1964, Oribatei made up 45% and Collembola 10.5% on the bark of the same tree species. In the control area not burned since 1964, Lepidoptera made up 21% and Phoridae (Diptera) 18.8% on the bark of *Q. macrocarpa*. Large differences can be seen in the community structure of the arthropods inhabiting the bark of trees in relation to the frequency of fire. On the bark of *Q. ellipsoidalis* in the area burned 20 times, Lepidoptera made up 29.3% of all collected arthropods and Chironomidae 12.6% (Table 1). In the area burned 3 times, Collembola made up 68.8% and Oribatei 19.6%. In the control area Lepidoptera made up 25.8% and Chironomidae and Phoridae 10% each. The bark of *Q. ellipsoidalis*, though similar to that of *Q. macrocarpa*, was dominated by different arthropod groups. However, in the area burned 3 times since 1964, the same arthropod groups were found on each species of oak (Table 1).

The main arthropod groups found on the trunks were determined to the genus or species level.

Table 1. Main arthropod groups (>5% of all animals collected) living exclusively on the bark of oaks in a North American savanna, in relation to the degree of disturbance, in the Cedar Creek Natural History Area, MN. Q.m. = *Quercus macrocarpa*, Q.e. = *Quercus ellipsoidalis*

Fire frequency	Qm 20	Qm 3	Qm 0	Qe 20	Qe 3	Qe 0
Oribatei		45.0	8.3		19.6	5.2
Acari (Non Oribatei)						7.5
Araneae		8.5	6.2			
Collembola		10.5			68.8	
Aphidina				11.7		
Cicadina	6.1					
Hymenoptera			7.2			7.5
Chironomidae	51.5	8.5		12.6		10.4
Mycetophilidae			5.1			
Phoridae			18.8			10.0
"Acalyptratae"				9.4		
Lepidoptera	21.9		21.0	29.3		25.8
Larvae div.				7.6		
Sum (%)	79.5	72.5	66.6	70.6	88.4	66.4

Oribatei

In total, 16 species of oribatid mites were found to live on the bark of *Q. macrocarpa* and *Q. ellipsoidalis* in the Cedar Creek Natural History Area (Fig. 1). Eight species were found on the bark of *Q. macrocarpa*, and the number of species (*N*) as well as the number of specimens (n/m^2) were highest on the area burned 3 times since 1964 (χ^2 test, $P < 0.05$) (Figure 1a).

On the bark of *Q. ellipsoidalis*, 12 species were found in the same area (Fig. 1b). In the area burned 3 times, the number of species (*N*) and the number of specimens (n/m^2) showed higher values than in the other study sites (burned 20 times since 1964, unburned) (Fig. 1b). Only four species of Oribatei (three of the genus *Eporibatula* and one of the genus *Scheloribates*) were found on the bark of both oak species (Fig. 1a, b).

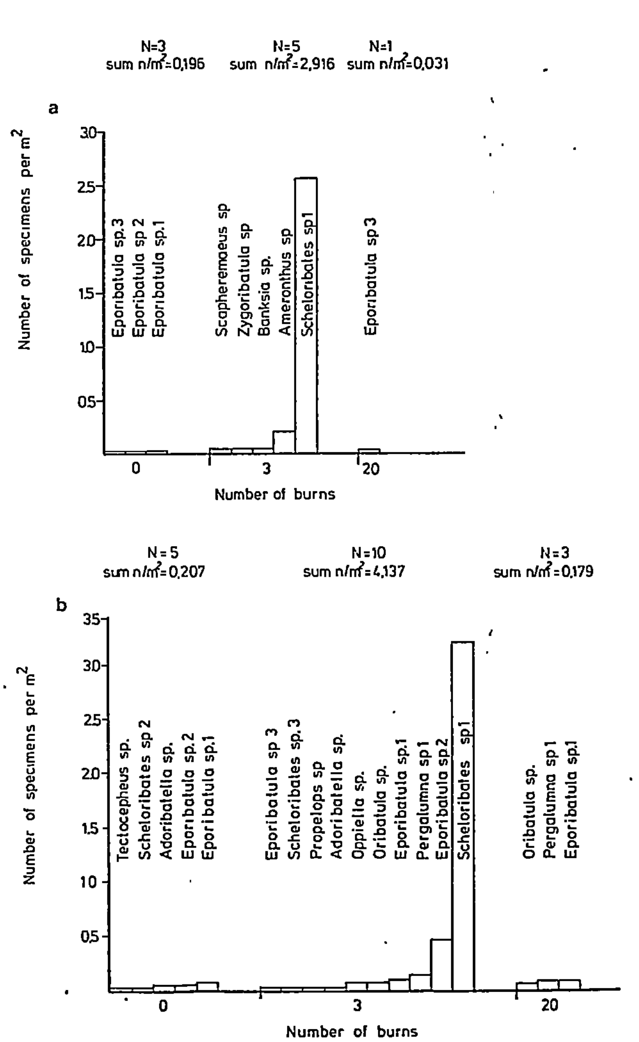


Fig. 1a, b. Oribatei on trunks of **a**, *Quercus macrocarpa* **b**, *Q. ellipsoidalis*. Number of specimens (*n*) per m^2 of bark of the given species (*N*) in relation to the number of burns in areas of the Cedar Creek Natural History Area

Diptera

Many different taxa of Diptera were found on the bark of *Q. macrocarpa* and *Q. ellipsoidalis* in the Cedar Creek Natural History Area (Fig. 2a, b). Tree trunks have different functions in the life cycles of the different spe-

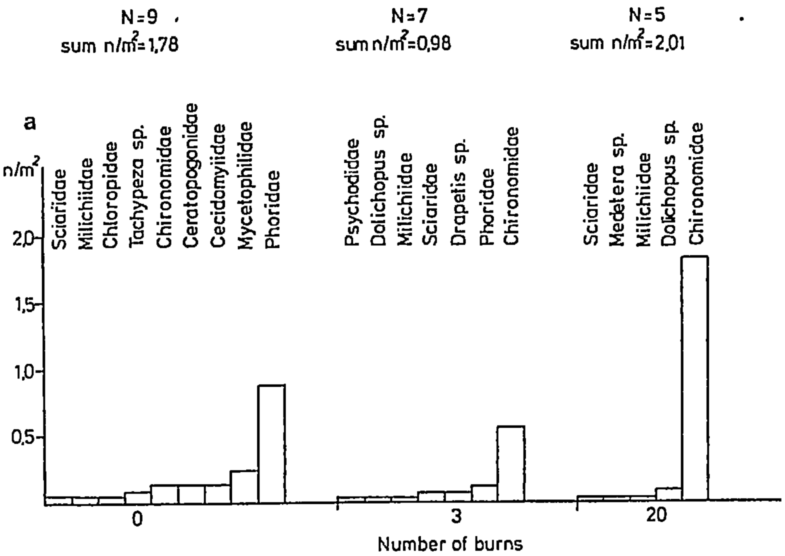
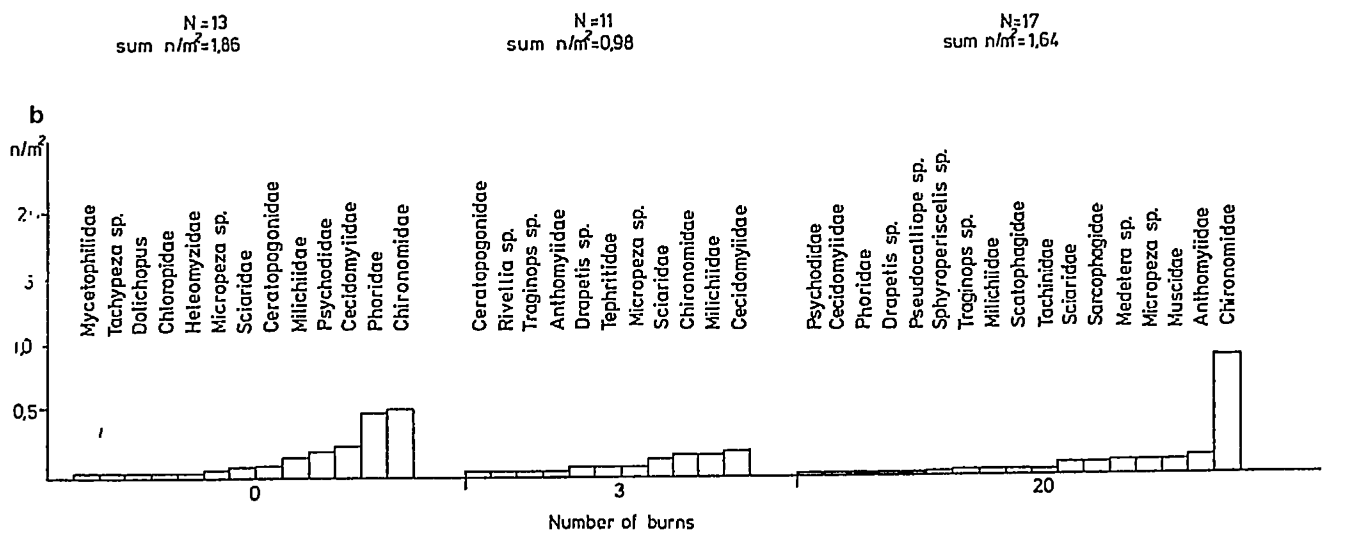


Fig. 2a, b. Diptera on trunks of a, *Quercus macrocarpa* b, *Q. ellipsoidalis*. Number of specimens (*n*) per m^2 of bark of the given group (*N*) in relation to the number of burns in areas of the Cedar Creek Natural History Area



cies. For *Drapetis* and *Tachypeza* (Empididae), *Medetera* (Dolichopodidae), and *Micropeza* (Micropezidae), tree trunks are the hunting areas. For *Neurogona* (Dolichopodidae) tree trunks are mating grounds.

For some nocturnal species (e.g., Limoniidae and some Chironomidae) tree trunks are a resting area and the bark of trees provides places to hide during the day. These species are camouflaged very well on bark (cf Nicolai 1987b). Others, such as the large predator *Micropeza* (body length: 7.9 ± 0.2 mm), are very striking inhabitants.

In general, more taxa of Diptera were found on the bark of *Q. ellipsoidalis* than on the bark of *Q. macrocarpa*. This was true in both burned and unburned areas (Fig. 2a, b). For Diptera overall, no sharp differences were seen in the community structure on the bark of *Q. macrocarpa* and *Q. ellipsoidalis* in the different burned areas (Fig. 2). However, some groups of Diptera showed strong effects. Very few Chironomidae were found on the bark of *Q. ellipsoidalis* in the unburned area, but many were found in the burned areas (Fig. 3).

For *Micropeza* spp. (Micropezidae), the trunks of *Quercus ellipsoidalis* are the hunting ground. They establish a small hunting area on the trunk that is defended against other individuals of the same species. If no prey has been caught for several minutes, they leave their hunting area for another location on the same trunk or move to another trunk.

A strong relation exists between the number of *Micropeza* per m^2 of bark and the fire regime (Fig. 4). The number of individuals per trunk or per m^2 of bark increases from the closed forest (control area) to the open savanna areas (Fig. 4). This species of *Micropeza* occurs in much higher numbers on the trunks of *Q. ellipsoidalis* in the open savanna area. This may be seen as a typical example of the reaction of a species to the change of an environment through the influence of an abiotic factor, in this case the frequency of fires.

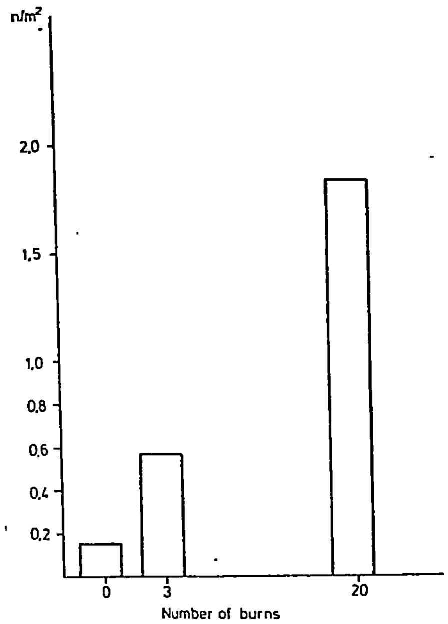


Fig. 3. Chironomidae (Diptera) on trunks of *Quercus macrocarpa*. Number of specimens (n) per m^2 of bark in relation to the number of burns in areas of the Cedar Creek Natural History Area

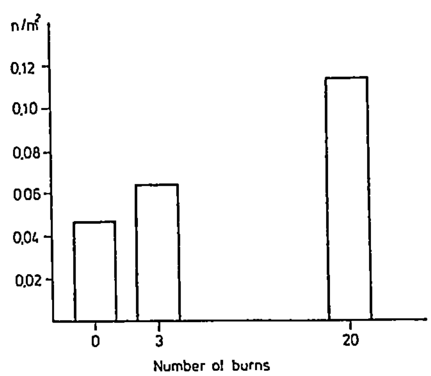


Fig. 4. *Micropeza* (Micropezidae, Diptera) on trunks of *Quercus ellipsoidalis*. Number of specimens (n) per m^2 of bark in relation to the number of burns in areas of the Cedar Creek Natural History Area .

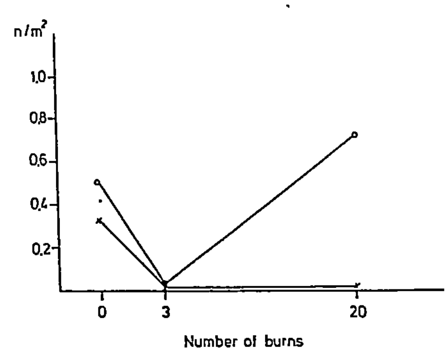


Fig. 5. One species of Pyralidae (o—o) and of Noctuidae (×—×) (Lepidoptera) on trunks of *Quercus ellipsoidalis*. Number of specimens (n) per m^2 of bark in relation to the number of burns in areas of the Cedar Creek Natural History Area

Lepidoptera

Incurvariidae, Pyralidae, and Noctuidae were the most important families of Lepidoptera found to live on the bark of *Q. macrocarpa* and *Q. ellipsoidalis*. Most of the species are nocturnal and use the bark to hide during the day. Two more examples of the reactions of bark-inhabiting arthropods are provided by Lepidoptera species. A species of Pyralidae is rare on the bark of *Q. ellipsoidalis* in the area burned 3 times, but lives on the bark of *Q. ellipsoidalis* in the more frequently burned area and in the unburned area (Fig. 5). A species of Noctuidae is restricted to bark of *Q. ellipsoidalis* in forested, unburned areas. It was rare in open savanna areas (Fig. 5).

General

The different arthropod taxa show various reactions to the frequency of fires. In the Cedar Creek Natural History Area the fires take place in early spring, at a time when many arthropods are still hibernating. For instance, Lepidoptera may not be affected directly by the fire, but rather through the influence of the fire on plant species on which they feed. True prairie plant species occur more frequently on the areas burned nearly every

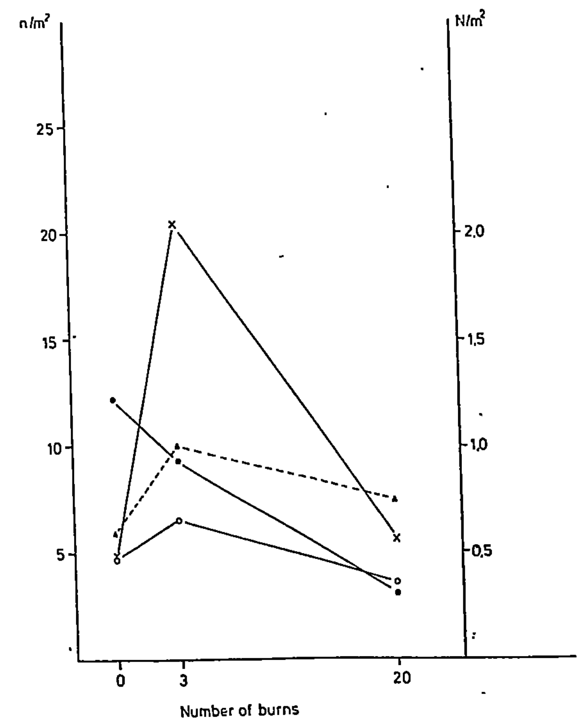


Fig. 6. Number of species (N/m^2) and number of specimens (n/m^2) on the bark of *Quercus macrocarpa* and *Q. ellipsoidalis* in relation to the number of burns in areas of the Cedar Creek Natural History Area. ×—× = number of arthropod specimens per m^2 on bark of *Q. ellipsoidalis*; △—△ = number of arthropod species per m^2 on bark of *Q. ellipsoidalis*; o—o = number of arthropod specimens per m^2 on bark of *Q. macrocarpa*; •—• = number of arthropod species per m^2 on bark of *Q. macrocarpa*

year (Tester 1989). If the food plant of a Lepidoptera species is affected, that species will also be affected. Other arthropods, like Oribatei, hibernate mainly as adults on the bark. Therefore, they are affected much more through the influence of spring fires, and the number of species as well as the number of specimens were highest on the bark of trees in the area burned only three times since 1964. Other major groups, e.g. Diptera, show less effect, but again strong reactions were found on a genus or species level within Diptera.

More species living on the bark of *Q. ellipsoidalis* were found in areas burned with a higher frequency (χ^2 test, $P < 0.05$) (Fig. 6). On the other hand, in the area with a moderate burn frequency many more specimens per m^2 inhabited the bark of *Q. ellipsoidalis* (χ^2 test, $P < 0.01$). The numbers of arthropod species living on the bark of *Q. ellipsoidalis* are related to the frequency of burns (Fig. 6).

Similar results were found for the specimens living on the bark of *Q. macrocarpa* (χ^2 test, $P < 0.01$) (Fig. 6). However, in total fewer species were living on the bark of *Q. macrocarpa* than on the bark of *Q. ellipsoidalis*. The number of species living on the bark of *Q. macrocarpa* was highest in the unburned area and lowest in the area burned 20 times. The numbers of arthropod species living on the bark of *Q. macrocarpa* reflect the frequency of burns in the specific areas.

A moderate frequency of disturbance by fire in the case of the oak savanna in the Cedar Creek Natural History Area, maintains a high number of typical savanna arthropod species and a high number of specimens inhabiting the bark of the two species of oaks.

Discussion

The frequencies of fires in European forests (Zackrisson 1977) and in North American forests (Frissell 1973) have been very much reduced by the influence of man in these regions. However, fire has been of highest importance and has determined vegetation and animal life for thousands of years (Swain 1973). In the North American oak savanna ecosystem fire is still a frequent abiotic factor (Curtis 1959). One main ecological function of bark is to protect the tree against fires, and the thermal insulating properties of the bark of the North American oak species *Q. macrocarpa* and *Q. ellipsoidalis* enable them to survive even annual burns (Nicolai 1990).

The arthropod fauna living on the bark of these oak species reacts to the different frequencies of burn. Typical or true savanna arthropod species increase in numbers on tree trunks in areas which are moderately burned (e.g. three times in 25 years). These arthropod species (e.g., species of the genus *Micropeza*, Diptera) live in even higher numbers on trunks of trees in areas which are burned with a higher frequency (e.g., 20 times in 25 years). They were rare on trunks of oaks in unburned areas.

An increase of true prairie and savanna plant species was observed in the areas burned with a higher frequency (Tester 1989). Phytophagous Lepidoptera, which feed as larvae on those savanna plant species and rest as adults on the trunks of oaks during the day, react in a more indirect way. Their presence on the trunks is influenced by the distribution of the forage plants used by their larvae.

Arthropods such as Oribatei, which hibernate mostly as adults on the trunks of trees, are directly influenced by early spring fires. More Oribatei species and individuals were found on the bark of oaks in the areas burned three times as on trunks in areas burned 20 times, or in unburned areas. Arthropod groups which are still hibernating during early spring, when the fires are conducted, seem to be less affected. Depending on the arthropod species and the time of burn, completely different reactions may result.

Elimination of the disturbance factor of fire in a North American oak savanna ecosystem for only 25 years gave rise to changes in arthropod communities living on the bark of *Q. macrocarpa* and *Q. ellipsoidalis*. On the bark of trees in an oak savanna not burned for more than 25 years the typical arthropod communities decreased in numbers, and arthropod species typical of the forest ecosystem increased. On the other hand, this fire program was initiated in 1964 to restore oak savanna from oak forests. This means that the typical bark-inhabiting arthropods of the savanna ecosystem were able to settle these new habitats within 25 years. Fire is necessary to maintain an arthropod community consisting of true savanna species living on bark of oaks in the North American savanna ecosystem.

In the mosaic cycle theory of ecosystems, disturbances are seen as natural components (Lang and Knight 1983; Remmert 1985, 1987; Schrempf 1986) and diversity in ecosystems is related to the degree of disturbance (Connell and Slatyer 1977; Connell 1978; Denslow 1980; Jacobs 1988; Whitemore 1989). Disturbances in ecosystems may be caused by fires (Stewart 1986; Uhl and Jordan 1984; Uhl et al. 1988; Zackrisson 1977), wind (Brewer and Merritt 1978), animals (Basey et al. 1988; Smith and Goodman 1987), phytophagy (Whitney 1984), disease (Menges and Loucks 1984), or even by volcanic eruptions (Spies and Franklin 1989). Most of these investigations deal with the effect of the disturbances on the vegetation.

For the different arthropod groups living on the bark of trees in a North American oak savanna, several adaptations exist with respect to the degree of disturbance by fire. Some species occur on trunks of trees only in undisturbed areas. They decrease in number on trunks of trees in moderate and heavily disturbed areas. Other species occur in high numbers only on trunks of oaks in moderately disturbed areas, and decrease in number on trunks of trees in undisturbed areas as well as in heavily disturbed areas. Again, other species increase in number on trunks of oaks in relation to the degree of disturbance. The more frequently an area is disturbed by fires, the more individuals of these species occur on the trunks of trees. The first type of species may be called "undisturbed-adapted", the second type of species may be called "disturbance-adapted", and the third type of species may be called "true fire-adapted."

On the whole, a higher number of disturbance-adapted species live on the bark of trees, and fewer true fire-adapted species and undisturbed species occur in the Cedar Creek Natural History Area.

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